Herbivory and fire interact to affect forest understory habitat, but not its use by small vertebrates

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Abstract

Herbivory and fire are two disturbances which often co-occur, but studies of their interactive effects are rare outside of grassland ecosystems. We experimentally tested the interactive effects of prescribed fire and macropod herbivory on forest understory vegetation and its vertebrate fauna. Fire and herbivory interacted synergistically to affect forest understory vegetation, with palatable plants showing poor post-fire recovery in un-fenced sites compared with herbivore exclusion sites. Despite this strong interactive effect on vegetation, small vertebrates responded to the individual, and not the interactive effects of disturbance. The native insectivorous mammal *Antechinus stuartii* was more frequently encountered on large herbivore exclusion sites, as was the introduced European rabbit. In contrast, the small skink *Lampropholis delicata* was more common on sites with high densities of large herbivores. Skinks, snakes and European rabbits were also more active on burnt than unburnt sites. Our results suggest that it may be necessary to manage the macropod herbivore population after fire to prevent the decline of palatable plants, and maintain the dense habitat required by some small mammals. However, as the invasive rabbit was most active in macropod-free sites after fire, any management must include control of both types of herbivores. A mix of understory densities may also need to be maintained to ensure the persistence of species preferring more open habitats. Our study demonstrates that interactive effects of disturbance on vegetation communities may not lead to predictable effects on animals, and highlights the importance of considering both multiple stressors, and multiple species, in the management of disturbance regimes.

Keywords

Disturbance interaction, browsing, grazing, indirect effects, kangaroo, synergistic effects

Introduction

Disturbance regimes play a central role in ecosystem dynamics (Willig and Walker, 1999). However, in many parts of the world, natural disturbance regimes have been disrupted, with unwanted outcomes for biodiversity (Hobbs and Huenneke, 1992, Sinclair and Byrom, 2006). Thus, many biodiversity conservation programs aim to reinstate natural disturbance regimes (Fuhlendorf *et al.*, 2010, Noss *et al.*, 2006), but achieving this in systems where multiple disturbances co-occur may be difficult. Co-occurring disturbances can interact to produce distinctly different outcomes from what would be expected based on individual effects (Didham *et al.*, 2007, Tylianakis *et al.*, 2008) and a poor understanding of these interactions can lead to unexpected and undesirable management outcomes (Lindenmayer *et al.*, 2010, Tylianakis *et al.*, 2008).

The importance of disturbance interactions for structuring grasslands and heathlands has been widely recognised, and re-establishing fire-grazing interactions is identified as a priority for maintaining biodiversity in these habitats (Fuhlendorf *et al.*, 2010, Van Langevelde *et al.*, 2003). However, understanding of how fire and herbivory interact to affect species in forested habitats remains limited (Foster, Barton and Lindenmayer, 2014, Royo *et al.*, 2010, Wisdom *et al.*, 2006). As the interactive effects of fire and herbivory depend on the scale, intensity and timing of these disturbances, the outcome of interactions can be highly variable (Fuhlendorf *et al.*, 2010, Wisdom *et al.*, 2006). For example, at a local-scale, deer browsing after fire supressed dominant shrub species, increasing herbaceous plant richness in a forest understory (Royo *et al.*, 2010). Conversely, heavy macropod herbivory following fire limited grass and forb recovery (Tuft, Crowther and McArthur, 2012). At a larger scale, Bailey and Whitham (2002) found that elk (*Cervus canadensis*) browsed more heavily in areas of aspen (*Populus tremuloides*) that burned at high intensity, compared with moderate intensity. This

heavy browsing reversed the positive effect of browsing on arthropod richness that occurred after moderate intensity fire. While such studies indicate that fire-herbivory interactions are likely to be prevalent in forested ecosystems (Royo and Carson, 2006), investigations of animal responses to the combined effects of these disturbances remain rare (Foster *et al.*, 2014, Wisdom *et al.*, 2006).

We combined prescribed fire and large herbivore exclusion treatments to test the interactive effects of fire and herbivory on understory vegetation and small vertebrates in a temperate forest ecosystem. As the management of disturbances is often targeted at plants, with the assumption that this will also cater for the needs of animals (Clarke, 2008), it is important to understand whether such assumptions are valid, and whether fauna respond in a predicable way to disturbances. Our study addressed the following questions: (1) How do fire, herbivory and their interaction affect understory habitat structure at the site level? (2) How do these disturbances affect site occupancy by small vertebrate fauna? We expected that vertebrate species would respond differently to the experimental treatments due to differences in their habitat and dietary preferences, and that these responses would be mediated by changes in vegetation structure. For example, we expected that both fire and herbivory would reduce understory cover, and lead to negative effects on site occupancy by vertebrates preferring dense understory habitats (Table 1). We provide recommendations for biodiversity conservation based on our findings.

Materials and methods

Study site

We conducted our study in Booderee National Park (BNP); a ~6 500 ha peninsula in south-eastern Australia (35°10′S, 150°40′E). We established sites within *Eucalyptus pilularis* forest, which is the most widespread vegetation type in BNP (Taws, 1998). An intensive fox (*Vulpes*

vulpes) baiting program has been conducted in BNP since 1999 to protect native species from predation (Dexter *et al.*, 2012). Over the last decade, there has been a tenfold increase in native herbivores in BNP (predominantly swamp wallaby, *Wallabia bicolor,* and eastern grey kangaroo, *Macropus giganteus*), which is attributed to reduced predation by foxes (Lindenmayer *et al.*, 2014). Small-scale exclosure trials indicate that this high abundance of herbivores could be driving changes in vegetation composition (Dexter *et al.*, 2013), and there is concern about flow-on effects for smaller vertebrates, which include a number of threatened species (Dexter *et al.*, 2012). As fire is a naturally occurring disturbance within BNP, occurring both as wildfire and low-intensity prescribed burning (Lindenmayer *et al.*, 2008), it is important to understand how native herbivores interact with fire regimes.

Study design

We quantified the interactive effects of fire and herbivory on vegetation and small vertebrates using a randomised blocked experiment. We combined three levels of large herbivore exclosure and two levels of burning treatment in a factorial design (Appendix 1). We replicated each treatment combination across four blocks to give 24 sites. For the exclosure treatments, we excluded macropod herbivores from 25 × 25 m sites, using 1.1 m tall wire fencing, in June 2012. We created three levels of herbivore exclosure treatment: high activity (open treatment – no fence), intermediate activity (partial treatment – sites were fenced but gates opened and closed at two month intervals to simulate lower herbivore pressure), and no large herbivores (exclosure treatment). For the burnt treatments, we conducted 50 × 50 m burns in August 2012, with the 25 x 25 m site in the centre of the burnt area. Fire was low-intensity, removing approximately 95% of understory vegetation and did not reach the canopy (scorch height 1.5 - 4 m) or burn large logs.

Data collection

We surveyed understorey vegetation prior to treatment in April/May 2012 and repeated surveys biannually until May 2014. We sampled four 3 × 3 m quadrats in each site, with each quadrat at least 1.5 m from the fence. We recorded four vegetation variables, representing important attributes of fauna habitat; total understorey projective cover (%), projective cover of bracken (*Pteridium escelentum*) (%), understorey height (averaged across 10 locations per quadrat using the stick-and-disc method of Smit *et al.* (2001); disc 100 mm diameter, 4.7 g weight) and litter depth (averaged across10 locations per quadrat).

We surveyed macropod herbivore activity by counting scats along two 25 × 2 m transects (100 m^{-2}) per site, summing counts to give one count per site. As macropods defecate more while feeding than resting (Johnson, Jarman and Southwell, 1987), pellet counts can give a comparative measure of macropod feeding pressure between sites (Howland *et al.*, 2014). We surveyed transects every two months from August 2012 to May 2014, removing scats after each survey to avoid re-counting. We also monitored European rabbit (*Oryctolagus cuniculus*) activity using these transects, counting the number of rabbit diggings every two months from June 2013 to May 2014.

We surveyed site use by small mammals through live trapping in April/May 2012 and then every six months until May 2014. For each survey, we set eight Elliott traps per site for four consecutive nights. We ear marked animals with a permanent marker to identify recaptures within a survey.

We monitored reptiles using iron sheeting as artificial substrates. We set out four 1 × 1 m sheets per site in July 2012, and checked them on two consecutive mornings approximately every two months from October 2012 to May 2014. To minimise biases due to time of day,

125 we rotated the order of site checking so that each site had one early morning and one late
126 morning check per sampling period. To avoid non-independence of counts within a survey,
127 we used the maximum value of the two consecutive counts for each species. Weather
128 conditions meant that some surveys returned few individuals. Therefore, for data analysis, we
129 excluded surveys with fewer than three detections for that species.
130
131 To measure arthropod prey availability, we sampled ground-dwelling beetles and spiders
132 using pitfall traps, counting the total captures per trap. We deployed four 250ml (100 mm
133 diameter) traps per site (2/3 filled with non-toxic polyethylene glycol solution) for two weeks
134 in November 2012 and 2013.
135
136 ***Data analysis***
137 To assess how fire-herbivory interactions affected habitat structure (question 1), and fauna
138 occupancy (question 2) we tested treatment effects on dependent variables using linear
139 mixed models (LMMs) for vegetation variables and generalised linear mixed models
140 (GLMMs) with Poisson errors for animal counts. Vegetation variables were understory cover
141 (%), understory cover excluding bracken (%, total understory cover minus cover of bracken),
142 understory height (m), and leaf litter depth (mm). We analysed understory cover excluding
143 bracken because bracken is a dominant, unpalatable species which could mask responses of
144 other plants. Bracken also provides little of the ground-level structure important for small
145 vertebrates (Bennett, 1993). Animal count variables were macropod scats, rabbit diggings,
146 antechinus captures, delicate skink (*Lampropholis delicata*) and eastern small-eyed snake
147 sightings (*Cryptophis nigrescens*), and spider and beetle captures.
148
149 We fitted each dependent variable with the full fixed effects model of
150 herbivores*burning*time, and random effects of block/site/quadrat for vegetation and

block/site for animal variables to account for the repeated measures. A first-order auto-regressive covariance structure on the random effects was trialled for the vegetation LMMs but was not used as it did not improve model fit ($\Delta AIC < 2$, Pinheiro and Bates, 2000). We did not define a covariance structure for animal responses as inspection of residuals indicated little evidence of temporal autocorrelation, and methods for fitting such structures with GLMMs are not well developed (Zuur *et al.*, 2009). We used Akaike information criterion, corrected for small sample size (AICc), to select the most parsimonious model from all possible subsets of the full model (19 models) (Burnham and Anderson, 2002). If models within two AICc of the top ranked model included predictors not included in the top model, we also discussed these alternate models. We excluded pre-treatment surveys from analyses to avoid spurious time × treatment interactions.

The properties of some animal variables meant that adjustments to the full model were necessary. Specifically, to adjust for over-dispersion of macropod scat data ($\varphi = 6.9$), rabbit digging data ($\varphi = 2.7$) and arthropod data ($\varphi = 3.1$), we added an observation-level random effect to the models for these variables (Harrison, 2014). Further, for the macropod model, we divided the partial herbivore treatment into two categories: partial – open months, and partial – closed months, to better describe this treatment. As there were low numbers of macropod scats in exclosure and partial – closed month treatments, they were excluded from this analysis. For the GLMM of antechinus captures, we ran model selection on all subsets of the full model of herbivores*burning*time, plus an alternate model with 'season' substituted for 'time' (giving 33 different models for comparison). This accounted for the strong seasonal variation in antechinus abundance (Lazenby-Cohen and Cockburn, 1991). Finally, as low mean counts for the two reptile species meant some models including the burn.time fixed effect did not converge, we excluded five models for the delicate skink and three models for the small-eyed snake from model comparisons. LMMs were performed using the lme

function in the package MASS, GLMMs using the glmer function in the package lme4 and AICc model ranking using the package AICcmodavg, within R version 3.0.1 (R Core Team, 2013).

Results

Vegetation structure

Vegetation structure responded both to the burning and herbivore exclosure treatments, as well as their interaction (Table 2). Understory vegetation cover at unburnt sites declined in open and partial treatments over time, but remained stable in exclosure sites (Fig. 1a). After an initial reduction after fire, a similar decline was observed for burnt, open sites. However, burnt partial and exclosure sites remained stable. (Fig. 1a, Appendix 2). When bracken was excluded from understory cover, there was a strong exclosure × time interaction, as cover on open and partial exclosure sites declined or remained low, while on full exclosure sites cover increased through time (Fig. 1b, Appendix 2). The burning × time interaction was also important, as non-bracken vegetation increased over time on all burnt sites. Compared with other treatments, burnt, open sites had a high proportion of bracken, with very little non-bracken vegetation present across all time periods (Fig. 1b). Both understory height and leaf litter depth responded to the burning × time interaction, but not to any other interaction terms (Table 2). Understory height was reduced by fire but had recovered after 21 months (Fig. 2a). Litter depth recovered more slowly, remaining lower in burnt than unburnt sites across all time periods (Fig. 2b). The second ranked model for understory height also included an exclosure main effect, where vegetation was slightly taller on exclosure than on open sites (Appendix 2).

Vertebrate responses

Exclosure treatments successfully excluded macropod herbivores, with very low scat counts in exclosure treatments (**Error! Bookmark not defined.**$\bar{x}$ = 0.71 ± 0.52). When partial treatment gates were open, scat counts were 56% lower in partial than in open treatments (Fig. 3a). Macropods also responded to burning, showing higher activity in burnt than unburnt sites (Table 2, Fig 3). There were three competing models for rabbit diggings, with models including time, time plus exclosure and time plus burning all explaining similar levels of variation in the data (Table 2). Rabbit activity peaked in summer and tended to be higher in sites without macropods (partial and full exclosure treatments) and in burnt sites (Fig. 4, Appendix 2).

Brown antechinus captures were highest in herbivore exclusion sites, and in Autumn (May) surveys (Table 2, Fig. 5). The second ranked model also included burning as a fixed effect (Table 2), where antechinus captures were slightly lower in burnt than unburnt sites (Appendix 2). Both the delicate skink and the eastern small-eyed snake were encountered more frequently in burnt sites than unburnt sites (Table 2, Fig. 6, Appendix 2). Delicate skink numbers also tended to be higher in open and partial than in full exclosure sites and were higher in the first survey (three months post-fire), than at any other time (Table 3, Fig, 6). Beetles and spiders captures were 65% higher in the first year (2012, **Error! Bookmark not defined.**$\bar{x}$ = 31.3 ± 3.1) than the second (2013, $\bar{x}$ = 18.9 ± 1.96), and the second ranked model indicated that captures were also slightly higher in burnt than in unburnt sites (Table 2, Appendix 2).

Discussion

Fire and herbivory can interact strongly in space and time to shape the structure of vegetation communities (Koerner and Collins, 2014, Royo and Carson, 2006, Van Langevelde *et al.*,

225 2003). However, animal responses to the fire × herbivory interaction are rarely studied (but
226 see Fuhlendorf *et al.*, 2010, Kimuyu *et al.*, 2014, Kutt and Woinarski, 2007). In our
227 experimental test of the interactive effects of fire and large herbivores, we found that forest
228 understory structure responded to the fire × herbivore exclosure interaction, but vertebrate
229 site occupancy was affected only by the individual effects of disturbance. This suggests that
230 local changes in vegetation structure may not be an adequate predictor of animal responses to
231 disturbance and that animals warrant individual consideration for the management of
232 ecosystems that are subject to both recurring fire and herbivory.
233
234 ***Question 1: Changes to habitat structure***
235 As expected, fire and herbivory both affected habitat structure, and effects differed with
236 disturbance type. The limited recovery of non-bracken vegetation on burnt sites with high
237 densities of large herbivores (Fig. 1), was consistent with previous studies (Meers and
238 Adams, 2003, Tuft *et al.*, 2012). Both of these previous studies attributed the stronger effect
239 of herbivory on burnt sites to greater herbivore pressure, driven by the attraction of
240 herbivores to the fresh plant growth following fire. This is a commonly reported mechanism
241 explaining fire × herbivore interactions (Klop, van Goethem and de Iongh, 2007), for which
242 we also found evidence, as indicated by macropod activity being greatest on recently burnt
243 sites (Fig. 2b).
244
245 In contrast to the non-bracken vegetation, bracken recovered well in burnt, open sites, and
246 made up a large proportion of the vegetation in these sites (Fig. 1). Bracken can regenerate
247 rapidly following fire and suppress other plants. However, after an initial post-fire pulse,
248 bracken cover usually declines over time, as other plants become dominant (Tolhurst and
249 Turvey, 1992). Our results indicate that abundant macropod herbivores may be disrupting this
250 successional process by selectively feeding on more palatable vegetation, maintaining the

bracken-dominated understory. As prescribed fire is commonly used in this system to reduce forest fuel loads and promote vegetation heterogeneity and floristic diversity (Morrison *et al.*, 1996), our results suggest that herbivore management following fire may be important to maintain a heterogeneous forest flora.

Question 2: Habitat use by vertebrates

Despite the strong effect of the fire × herbivory interaction on vegetation, habitat use by vertebrates was affected only by the individual effects of disturbances and not their interaction. The increased rabbit activity we observed on herbivore exclusion and recently burnt sites was consistent with previous studies of small herbivore responses to large herbivore removal (Keesing, 1998) and fire (Leigh *et al.*, 1987, Moreno and Villafuerte, 1995). Competitive release of small herbivores following a reduction in large herbivore densities can result in increased herbivory by small herbivores, with subsequent impacts on vegetation communities (Lagendijk, Page and Slotow, 2012). Our results suggest that control of native macropod herbivores may favour introduced rabbits, particularly after fire when fresh plant growth is abundant. Therefore, management of the native herbivore population should carefully consider the potential for competitive release of the European rabbit, which is a destructive pest species in Australia (Davey *et al.*, 2006).

Antechinus responded positively to large herbivore exclusion, with more individuals captured in sites without macropod herbivores, regardless of burning treatment. Despite the small size of our exclosures, this response likely indicates a preference for herbivore exclusion areas, as antechinus have small foraging ranges (approximately 0.4 ha for females and 0.9 ha for males, Lazenby-Cohen and Cockburn, 1991). Further, our result is consistent with Pedersen *et al.* (2014), who found that antechinus captures were negatively correlated with wallaby density. The preference of antechinus for sites without large herbivores may have been due

277 to the dense understory cover in exclosure sites (Bennett, 1993, Knight and Fox, 2000),
278 providing increased foraging habitat (antechinus are scansorial) and/or greater protection
279 from predators (e.g. Stokes *et al.*, 2004). Other studies have found that some small mammal
280 species prefer habitats with lower densities of large herbivores (Bush *et al.*, 2012, Keesing,
281 1998, Kutt and Gordon, 2012), but our study is the first to experimentally demonstrate this
282 response to macropod herbivores.
283
284 Contrary to other studies from south-eastern Australia (Fox, 1982, Lindenmayer *et al.*, 2008),
285 we found only weak support for a negative response of antechinus to fire. This was likely due
286 to the low intensity, small-scale fires used in our study. The availability of arthropod prey
287 (Table 2, Appendix 2), combined with the persistence of logs and the proximity of unburnt
288 vegetation to burnt areas in our study, may have sufficiently maintained habitat quality for
289 antechinus. It is likely that antechinus may have responded more strongly to a larger-scale, or
290 higher intensity burn (Lindenmayer *et al.*, 2008, Penn *et al.*, 2003).
291
292 Delicate skinks were more common in open than in herbivore exclusion sites, and both
293 delicate skinks and small-eyed snakes were more common in burnt than unburnt sites. The
294 negative response of delicate skins to herbivore exclusion was likely due to increased shading
295 from recovering vegetation, which could have reduced the thermal suitability of the
296 environment for this heliothermic species (Howard, Williamson and Mather, 2003). The
297 positive response of the delicate skink to burning was contrary to our expectation for this
298 species, which generally recovers slowly from fire, in response to the slow accumulation of
299 leaf litter (Taylor and Fox, 2001). Our result may therefore reflect a change in micro-habitat
300 use following burning, rather than a change in site occupancy. Burning reduced litter depth,
301 and in the absence of suitable leaf-litter habitat, the delicate skink may have increased its use

of the artificial survey substrates for shelter, basking and foraging, as found by Croft, Reid and Hunter (2010).

A lack of alternative refuges also may explain the higher numbers of small-eyed snakes under the artificial substrates in burnt sites. However, there are two other possible explanations for this response: First is that the small-eyed snake was more common after burning as a result of reduced shading of substrates, which provided warmer, more desirable diurnal refuges (Webb *et al.*, 2004). Second, the density of skinks, a key prey item for small-eyed snakes (Shine, 1984), may have attracted snakes to the substrates in burnt sites. Previous studies of small-eyed snakes show that reduced shading after fire can improve the thermal properties of diurnal refuges (Webb *et al.*, 2005), but large wildfire can lead to population declines, possibly due to increased predation (Webb and Shine, 2008). While the possible biases in our reptile sampling technique mean results should be interpreted with caution, the greater numbers of reptiles in burnt sites and skinks in the open treatments, indicate that maintaining areas of open understory may be important for the persistence of reptiles in these forests (Webb *et al.*, 2005).

Conservation implications

Our results have four key implications relevant to the conservation of ecosystems subject to both recurrent fire and herbivory. First, the dominance of bracken and limited recovery of other vegetation in burnt, open sites indicates that short-term management of abundant macropod herbivores following prescribed fire may be useful for the conservation of structurally and floristically complex vegetation. Second, the preference of antechinus for herbivore exclusion sites suggests that management of native herbivores to promote dense understory habitat is also likely to benefit small mammals dependent on such habitats. Third, the increased rabbit activity we observed on recently burnt sites, and sites without

328 macropods, suggests that any plan to improve the post-fire recovery of vegetation by
329 controlling native herbivores also should include management of rabbits. Fourth, the positive
330 response of reptiles to the open understory of burnt sites and sites with more macropods
331 differed from the antechinus response, and suggests that a mixed management scenario might
332 be more appropriate.
333
334 While our experiments were small-scale, the contrasting responses of different species to
335 herbivory and fire indicate that a mixed management strategy promoting a heterogeneous
336 understory may be important for the persistence of all species in our study. Heterogeneous
337 landscapes have commonly been suggested as a desired goal of land management, as such
338 landscapes are more likely to allow the co-existence of species with different niches, as well
339 as species that require a mix of habitats (Law and Dickman, 1998, Stein, Gerstner and Kreft,
340 2014). In Australian landscapes, fire patch-mosaics have been recommended to promote
341 fauna diversity, although key questions around the appropriate spatial and temporal scales of
342 such mosaics remain unanswered (Allouche *et al.*, 2012, Clarke, 2008, Driscoll *et al.*, 2010).
343 While not designed to address questions of spatial scale, our study suggests that maintaining
344 a mix of habitat types and conditions may be important for fauna in forested systems.
345
346 Although both fire and herbivory are often actively managed in forested systems (Gordon,
347 Hester and Festa-Bianchet, 2004, Morrison *et al.*, 1996), these processes are usually
348 considered independently (Royo and Carson, 2006, Wisdom *et al.*, 2006). However, the
349 interactive effects of fire and herbivory observed in our study indicate that integrating large
350 herbivore management with fire management practices is likely to be important for achieving
351 vegetation heterogeneity in forests. This could be through the fire-dependent management of
352 herbivores (e.g. controlling large herbivores across only part of a burn or after only some
353 prescribed burns), or through planning fires to consider large herbivore behaviour (e.g.

reducing the edge-area ratio of prescribed burns, as macropods can be reluctant to enter open areas and so feed more heavily at the edge (While and McArthur, 2006)). Our study shows the value of experimental studies that quantify disturbance responses both individually and collectively, and highlights the importance of considering both multiple stressors, and multiple species, in the management of disturbance regimes.

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365 ## References

366 Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M. & Kadmon, R. (2012). Area–
367 heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the*
368 *National Academy of Sciences* 109, 17495-17500.

369 Bailey, J. K. & Whitham, T. G. (2002). Interactions among fire, aspen, and elk affect insect
370 diversity: Reversal of a community response. *Ecology* 83, 1701-1712.

371 Bennett, A. F. (1993). Microhabitat use by the long-nosed potoroo, *Potorous tridactylus*, and
372 other small mammals in remnant forest vegetation, south-western Victoria. *Wildl. Res.*
373 20, 267-285.

374 Bragg, J. G., Taylor, J. E. & Fox, B. J. (2005). Distributions of lizard species across edges
375 delimiting open-forest and sand-mined areas. *Austral Ecol.* 30, 188-200.

376 Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a*
377 *practical information-theoretic approach*. 2nd ed. edn. New York: Springer-Verlag.

378 Bush, E. R., Buesching, C. D., Slade, E. M. & Macdonald, D. W. (2012). Woodland recovery
379 after suppression of deer: cascade effects for small mammals, wood mice (*Apodemus*
380 *sylvaticus*) and bank voles (*Myodes glareolus*). *PLoS ONE* 7, e31404.

381 Catling, P. & Burt, R. (1995). Studies of the ground-dwelling mammals of eucalypt forests in
382 south-eastern New South Wales: the effect of habitat variables on distribution and
383 abundance. *Wildl. Res.* 22, 271-288.

384 Clarke, M. F. (2008). Catering for the needs of fauna in fire management: science or just
385 wishful thinking? *Wildl. Res.* 35, 385-394.

386 Croft, P., Reid, N. & Hunter, J. (2010). Experimental burning changes the quality of fallen
387 timber as habitat for vertebrate and invertebrate fauna: implications for fire
388 management. *Wildl. Res.* 37, 574-581.

389 Davey, C., Sinclair, A., Pech, R., Arthur, A., Krebs, C., Newsome, A., Hik, D., Molsher, R.
390 & Allcock, K. (2006). Do exotic vertebrates structure the biota of Australia? An
391 experimental test in New South Wales. *Ecosystems* 9, 992-1008.
392 Davis, N. E., Coulson, G. & Forsyth, D. M. (2008). Diets of native and introduced
393 mammalian herbivores in shrub-encroached grassy woodland, south-eastern Australia.
394 *Wildl. Res.* 35, 684-694.
395 Dexter, N., Hudson, M., James, S., MacGregor, C. & Lindenmayer, D. B. (2013). Unintended
396 consequences of invasive predator control in an Australian forest: Overabundant
397 wallabies and vegetation change. *PloS ONE* 8, e69087.
398 Dexter, N., Ramsey, D. L., MacGregor, C. & Lindenmayer, D. (2012). Predicting ecosystem
399 wide impacts of wallaby management using a fuzzy cognitive map. *Ecosystems* 15,
400 1363-1379.
401 Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A. & Ewers, R. M. (2007).
402 Interactive effects of habitat modification and species invasion on native species
403 decline. *Trends Ecol. Evol.* 22, 489-496.
404 Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J.,
405 Clarke, M. F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith,
406 D. A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J. E. M., Williams, R. J. &
407 York, A. (2010). Fire management for biodiversity conservation: Key research
408 questions and our capacity to answer them. *Biol. Conserv.* 143, 1928-1939.
409 Foster, C. N., Barton, P. S. & Lindenmayer, D. B. (2014). Effects of large native herbivores
410 on other animals. *J. Appl. Ecol.* 51, 929–938.
411 Fox, B. J. (1982). Fire and mammalian secondary succession in an Australian coastal heath.
412 *Ecology*, 1332-1341.

413 Fuhlendorf, S. D., Townsend, D. E., Elmore, R. D. & Engle, D. M. (2010). Pyric-herbivory to
414 promote rangeland heterogeneity: Evidence from small mammal communities.
415 *Rangeland Ecol. Manage.* 63, 670-678.
416 Gordon, I. J., Hester, A. J. & Festa-Bianchet, M. (2004). The management of wild large
417 herbivores to meet economic, conservation and environmental objectives. *J. Appl. Ecol.*
418 41, 1021-1031.
419 Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in
420 count data in ecology and evolution. *PeerJ* 2, e616.
421 Hobbs, R. J. & Huenneke, L. F. (1992). Disturbance, diversity, and invasion: Implications for
422 conservation. *Conserv. Biol.* 6, 324-337.
423 Howard, R., Williamson, I. & Mather, P. (2003). Structural aspects of microhabitat selection
424 by the skink *Lampropholis delicata*. *J. Herpetol.* 37, 613-617.
425 Howland, B., Stojanovic, D., Gordon, I. J., Manning, A. D., Fletcher, D. & Lindenmayer, D.
426 B. (2014). Eaten out of house and home: Impacts of grazing on ground-dwelling
427 reptiles in Australian grasslands and grassy woodlands. *PLoS ONE* 9, e105966.
428 Johnson, C. N., Jarman, P. J. & Southwell, C. J. (1987). Macropod studies at Wallaby Creek.
429 5. Patterns of defecation by eastern gray kangaroos and red-necked wallabies. *Wildl.*
430 *Res.* 14, 133-138.
431 Keesing, F. (1998). Impacts of ungulates on the demography and diversity of small mammals
432 in central Kenya. *Oecologia* 116, 381-389.
433 Kimuyu, D. M., Sensenig, R. L., Riginos, C., Veblen, K. E. & Young, T. P. (2014). Native
434 and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant
435 mortality in an African savanna. *Ecol. Appl.* 24, 741-749.
436 Klop, E., van Goethem, J. & de Iongh, H. H. (2007). Resource selection by grazing
437 herbivores on post-fire regrowth in a West African woodland savanna. *Wildl. Res.* 34,
438 77-83.

439 Knight, E. H. & Fox, B. J. (2000). Does habitat structure mediate the effects of forest
440 fragmentation and human-induced disturbance on the abundance of *Antechinus stuartii*?
441 *Aust. J. Zool.* 48, 577-595.
442 Koerner, S. E. & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on
443 grassland plant communities in North America and South Africa. *Ecology* 95, 98-109.
444 Kutt, A. S. & Gordon, I. J. (2012). Variation in terrestrial mammal abundance on pastoral and
445 conservation land tenures in north-eastern Australian tropical savannas. *Anim. Conserv.*
446 15, 416-425.
447 Kutt, A. S. & Woinarski, J. C. Z. (2007). The effects of grazing and fire on vegetation and the
448 vertebrate assemblage in a tropical savanna woodland in north-eastern Australia. *J.*
449 *Trop. Ecol.* 23, 95-106.
450 Lagendijk, G., Page, B. R. & Slotow, R. (2012). Short-term effects of single species browsing
451 release by different-sized herbivores on sand forest vegetation community, South
452 Africa. *Biotropica* 44, 63-72.
453 Law, B. S. & Dickman, C. R. (1998). The use of habitat mosaics by terrestrial vertebrate
454 fauna: implications for conservation and management. *Biodiversity & Conservation* 7,
455 323-333.
456 Lazenby-Cohen, K. A. & Cockburn, A. (1991). Social and foraging components of the home
457 range in *Antechinus stuartii* (Dasyuridae: Marsupialia). *Aust. J. Ecol.* 16, 301-307.
458 Leigh, J., Wimbush, D., Wood, D., Holgate, M., Slee, A., Stanger, M. & Forrester, R. (1987).
459 Effects of rabbit grazing and fire on a sub-alpine environment .I. Herbaceous and
460 shrubby vegetation. *Aust. J. Bot.* 35, 433-464.
461 Lindenmayer, D., MacGregor, C., Dexter, N., Fortescue, M. & Beaton, E. (2014). *Booderee*
462 *National Park, The Jewel of Jervis Bay*. Collingwood, Australia: CSIRO Publishing.

463 Lindenmayer, D. B., Likens, G. E., Krebs, C. J. & Hobbs, R. J. (2010). Improved probability
464 of detection of ecological “surprises”. *Proceedings of the National Academy of Sciences*
465 107, 21957-21962.
466 Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D.,
467 Montague-Drake, R., Cunningham, R., Brown, D., Fortescue, M., Dexter, N., Hudson,
468 M. & Gill, A. M. (2008). Contrasting mammal responses to vegetation type and fire.
469 *Wildl. Res.* 35, 395-408.
470 Meers, T. & Adams, R. (2003). The impact of grazing by eastern grey kangaroos *(Macropus*
471 *giganteus*) on vegetation recovery after fire at Reef Hills Regional Park, Victoria. *Ecol.*
472 *Manage. Restor.* 4, 126-132.
473 Moreno, S. & Villafuerte, R. (1995). Traditional management of scrubland for the
474 conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National
475 Park, Spain. *Biol. Conserv.* 73, 81-85.
476 Morrison, D. A., Buckney, R. T., Bewick, B. J. & Cary, G. J. (1996). Conservation conflicts
477 over burning bush in south-eastern Australia. *Biol. Conserv.* 76, 167-175.
478 Noss, R. F., Franklin, J. F., Baker, W. L., Schoennagel, T. & Moyle, P. B. (2006). Managing
479 fire-prone forests in the western United States. *Front. Ecol. Environ.* 4, 481-487.
480 Pedersen, S., Andreassen, H. P., Keith, D. A., Skarpe, C., Dickman, C. R., Gordon, I. J.,
481 Crowther, M. S. & McArthur, C. (2014). Relationships between native small mammals
482 and native and introduced large herbivores. *Austral Ecol.* 39, 236-243.
483 Penn, A. M., Sherwin, W. B., Lunney, D. & Banks, P. B. (2003). The effects of a low-
484 intensity fire on small mammals and lizards in a logged, burnt forest. *Wildl. Res.* 30,
485 477-486.
486 Pinheiro, J. & Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS*. New York, NY:
487 Springer-Verlag.

R Core Team (2013). *A language and environment for statistical computing*. Vienna, Austria. URL http://www.R-project.org/: R Foundation for Statistical Computing.

Royo, A. A. & Carson, W. P. (2006). On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* 36, 1345-1362.

Royo, A. A., Collins, R., Adams, M. B., Kirschbaum, C. & Carson, W. P. (2010). Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91, 93-105.

Shine, R. (1984). Reproductive biology and food habits of the Australian elapid snakes of the genus *Cryptophis*. *J. Herpetol.* 18, 33-39.

Sinclair, A. R. E. & Byrom, A. E. (2006). Understanding ecosystem dynamics for conservation of biota. *J. Anim. Ecol.* 75, 64-79.

Smit, R., Bokdam, J., den Ouden, J., Olff, H., Schot-Opschoor, H. & Schrijvers, M. (2001). Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecol.* 155, 119-127.

Stein, A., Gerstner, K. & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17, 866-880.

Stokes, V. L., Pech, R. P., Banks, P. B. & Arthur, A. D. (2004). Foraging behaviour and habitat use by Antechinus flavipes and Sminthopsis murina (Marsupialia: Dasyuridae) in response to predation risk in eucalypt woodland. *Biol. Conserv.* 117, 331-342.

Taws, N. (1998). *Fire and vegetation management in Jervis Bay Territory, Report*. Canberra: Environment Australia.

Taylor, J. E. & Fox, B. J. (2001). Disturbance effects from fire and mining produce different lizard communities in eastern Australian forests. *Austral Ecol.* 26, 193-204.

512 Tolhurst, K. G. & Turvey, N. D. (1992). Effects of bracken (*Pteridium esculentum* (forst. f.)
513 Cockayne) on eucalypt regeneration in west-central Victoria. *For. Ecol. Manage.* 54,
514 45-67.
515 Tuft, K. D., Crowther, M. S. & McArthur, C. (2012). Fire and grazing influence food
516 resources of an endangered rock-wallaby. *Wildl. Res.* 39, 436-445.
517 Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. (2008). Global change and
518 species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351-1363.
519 Van Langevelde, F., Van De Vijver, C. A. D. M., Kumar, L., Van De Koppel, J., De Ridder,
520 N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., Prins,
521 H. H. T. & Rietkerk, M. (2003). Effects of fire and herbivory on the stability of savanna
522 ecosystems. *Ecology* 84, 337-350.
523 Webb, J. K., Pringle, R. M., Shine, R. & Lannoo, M. J. (2004). How do nocturnal snakes
524 select diurnal retreat sites? *Copeia* 2004, 919-925.
525 Webb, J. K. & Shine, R. (2008). Differential effects of an intense wildfire on survival of
526 sympatric snakes. *J. Wildl. Manage.* 72, 1394-1398.
527 Webb, J. K., Shine, R., Pringle, R. M. & Lannoo, M. J. (2005). Canopy removal restores
528 habitat quality for an endangered snake in a fire suppressed landscape. *Copeia* 2005,
529 894-900.
530 While, G. M. & McArthur, C. (2006). Distance from cover affects artificial food-patch
531 depletion by macropod herbivores. *Wildl. Res.* 33, 565-570.
532 Willig, M. R. & Walker, L. R. (1999). Disturbance in terrestrial ecosystems: Salient themes,
533 synthesis, and future directions. In *Ecosystems of the World 16: Ecosystems of*
534 *Disturbed Ground*: 747-768. Walker, L. R. (Ed.). Amsterdam: Elsevier Science.
535 Wisdom, M. J., Vavra, M., Boyd, J. M., Hemstrom, M. A., Ager, A. A. & Johnson, B. K.
536 (2006). Understanding ungulate herbivory-episodic disturbance effects on vegetation
537 dynamics: Knowledge gaps and management needs. *Wildl. Soc. Bull.* 34, 283-292.

538 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects*
539 *models and extensions in ecology with R*. New York, USA: Springer.
540

Tables

Table 1. Predicted effects of fire and large herbivores on habitat and food resources for vertebrates and the corresponding predicted responses of two small mammal and two reptile species, based on their diet and habitat preferences. Habitat preferences are attributes which have been associated with higher abundance in forest habitat for that species.

Response group	Habitat preference	Diet	Predicted response	
			Fire	Herbivores
Habitat and food resources				
Understory cover			-	-
Understory height			-	-
Leaf litter depth			-	none
Fresh plant growth			+	-
Invertebrate prey			-	-
Vertebrates				
European rabbit (*Oryctolagus cuniculus*)	Open understory [a]	Forbs and grasses [b]	+	-
Brown antechinus (*Antechinus stuartii*)	Dense, complex understory [a,c] Tall understory [d] Abundant logs [d]	Invertebrates [c]	-	-
Delicate skink (*Lampropholis delicata*)	High canopy cover [e] Deep litter [f,g] Tall understory [g]	Invertebrates [e]	-	?
Eastern small-eyed snake (*Cryptophis nigrescens*)	Warm diurnal refuge [h]	Skinks [h]	+	?

[a]Catling and Burt (1995), [b] Davis, Coulson and Forsyth (2008), [c] Bennett (1993), [d] Knight and Fox (2000), [e] Bragg, Taylor and Fox (2005), [f] Taylor and Fox (2001), [g] Howard *et al.* (2003), ,[h] Webb *et al.* (2004),

548 Table 2. Model rankings for linear mixed models (LMMs, vegetation) and generalised linear
549 mixed models (GLMMs, animals), testing the fixed effects of burning (B - burnt or unburnt),
550 exclosure (E - open, partial or full exclosure), time (T - sampling event - categorical), and
551 their interactions on vegetation structure and animal occurrence. For brown antechinus, we
552 also ran model ranking on all subsets of a model with season (S - autumn or spring)
553 substituted for time (i.e. B*E*S), to account for the strong seasonal variation in the
554 abundance of this species. K is the number of parameters estimated in the model, Δ AICc is
555 the change in Aikaike's Information Criterion (corrected for small sample size) from the best-
556 ranked model. AICcWt is the Aikine Weight of the model, LL is the Log-likelihood.

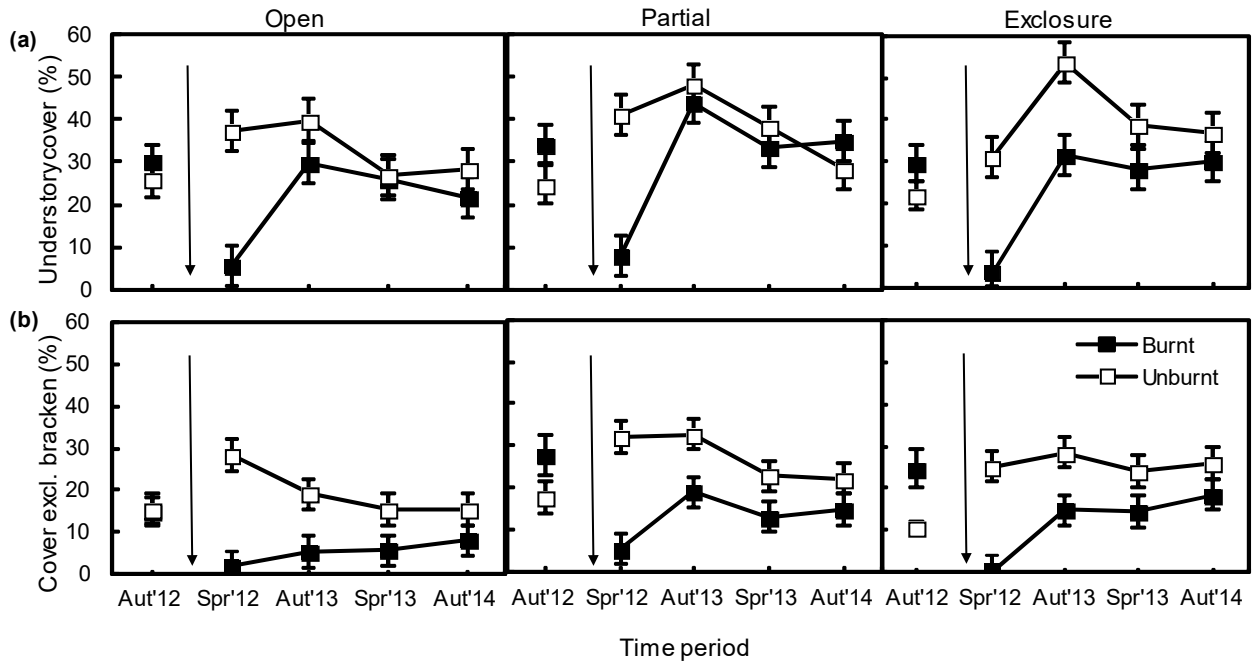
Data	Model terms	K	Δ AICc	AICcWt	LL
LMMs					
Understory cover	B + E + T + B:T + E:T + B:E + B:E:T	28	0	0.97	-1454.7
Cover excluding bracken	B + E + T + B:T + E:T	20	0	0.74	-1389.6
Vegetation height	B + T + B:T	12	0	0.61	266.5
	B + E + T + B:T	14	1.59	0.28	267.8
Litter depth	B + T + B:T	12	0	0.82	-429.5
GLMMs					
Macropod scats	B + E[a] + T	15	0	0.6	-500.6
Rabbit diggings	T	9	0	0.37	-441.0
	E + T	11	1.09	0.21	-439.2
	B + T	10	1.64	0.16	-440.7
Brown antechinus	E + season	6	0	0.36	-172.0
	B + E + season	7	1.4	0.18	-171.5
Delicate skink	B + E + T	13	1.01	0.46	-162.8
	B + T	11	1.35	0.39	-165.3
Eastern small-eyed snake	B	4	0	0.67	-60.4
Beetles and spiders	T	5	0	0.61	-187.4
	B + T	6	1.85	0.24	-187.0

[a] Compares only partial-open months with open treatment (see methods)

557

558

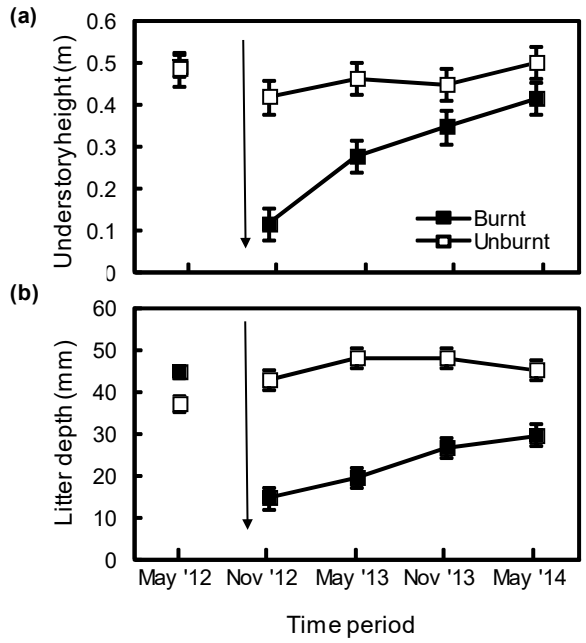
559 **Figures**



560

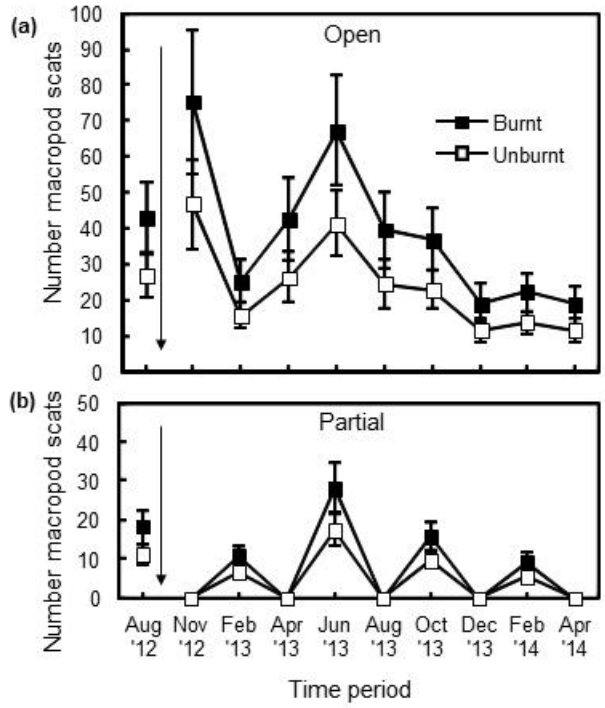
561 Figure 1. Vegetation structural responses to exclosure and burning treatments across
562 sampling periods, (a) total understory percent cover, and (b) understory percent cover,
563 excluding bracken (*Pteridium esculentum*). Values post-treatment are predicted means and
564 estimated SE from the top-ranked models. Pre-treatment data (May 2012) were not included
565 in the LMM, but are presented here (mean and SE) to allow comparison with post-treatment
566 data. Arrows indicate timing of prescribed burning.

567



568

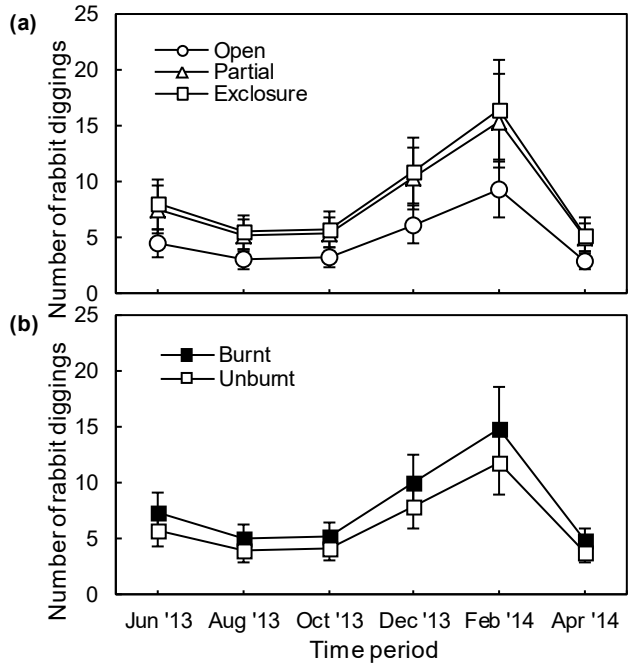
569 Figure 2. Response of understory height (a) and leaf litter depth (b) to burning treatment
570 across time periods. Values post-treatment are predicted means and SE from the top-ranked
571 models. Pre-treatment data (May 2012) were not included in the LMM, but are presented here
572 (mean and SE) to allow comparison with post-treatment data. Arrows indicate timing of
573 prescribed burning.



574

575 Figure 3. Number of macropod scats in burnt and unburnt sites through time in open (a) and
576 partial exclosure sites (b). Note that closed months of the partial exclosures (Nov 2012, Apr
577 2013 etc.), and full exclosure sites were not included in the analysis as means for this group
578 were too low to allow model fit. Values for open sites and partial-open months are predicted
579 means and estimated SE from the top-ranked model. Arrows indicate timing of prescribed
580 burning (note Aug '12 counts were after implementation of herbivory treatments but before
581 burning treatment).

582



583

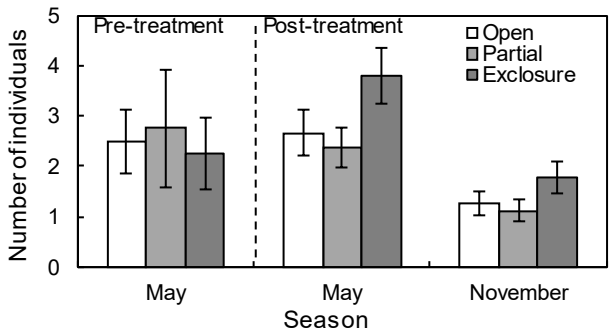
584 Figure 4. Number of rabbit (*Oryctolagus cuniculus*) diggings per site in the different

585 exclosure treatments (a) and burning treatments (b) over time. Values are predicted means

586 and estimated SE from the 2nd (a) and 3rd (b) ranked models respectively. The effect of time

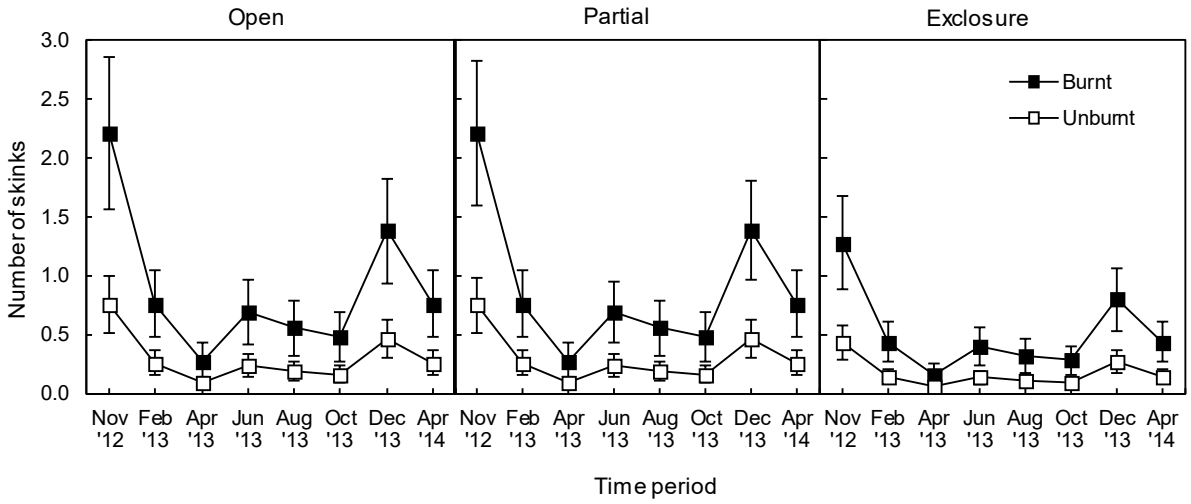
587 alone (first-ranked model) can be clearly seen in both plots.

588



589

590 Figure 5. Number of individual brown antechinus (*Antechinus stuartii*) captured per site in
591 different seasons and herbivory treatments. Values post-treatment are predicted means and
592 SE from the top-ranked model based on two years of data (November 2012 to May 2014).
593 Pre-treatment data (May 2012) were not included in the GLMM, but are presented here
594 (mean and SE) to allow comparison with post-treatment data.



595

596 Figure 6. Number of delicate skinks (*Lampropholis delicata*) detected under artificial

597 substrates in the different burning and exclosure treatments across time. Values are predicted

598 means and SE from the top-ranked model.